Predatory gastropod traces: a comparison of verified shallow-water and presumed deep-sea boreholes

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Abstract: The present study was based on a light microscopic examination of gastropod-type boreholes in shells of deep-sea mollusks dredged by the *Galathea* Expedition at stations off of southern Africa, east of India, in the Indonesian region, and off of southern Australia; the *Ingolf* Expedition in the North Atlantic; and the *Gosnold* survey off of the eastern coast of the United States. The morphology of these holes is closely similar to that of boreholes drilled by shallow-water naticodean and muricodean gastropods. This coincidence in form supports the conclusion that these deep-sea holes were also bored by gastropods. Boreholes, in shells dredged as deep as 2690 m, ranged in external diameter from 0.2-3.1 mm, were round, smooth-walled, and significantly smaller than those drilled by shallow-water gastropods. The presence of gastropod boreholes in prey shells from the deep sea is not surprising, as species of Naticidae, Muricidae, and Trophonidae, the first more commonly, have been dredged from several oceanic stations, naticids from as deep as 6860 m. In the present study, muricid-type boreholes were 1/7 as common as naticid-type holes, probably a reflection of the lower density of muricid species and the soft surface of much of the ocean floor, which, at least in shallow water, tends to inhibit muricid reproduction.

Key words: gastropods, predators, shell borers, boreholes, deep-sea

No one has yet observed living deep-sea predatory gastropods in the act of drilling holes in living deep-sea molluscan prey. Thus the few holes that have been reported as deep-sea boreholes (for example, Boone and Carriker, 1960; Knudsen, 1970), have been so named because of their apparent likeness to those excavated under laboratory conditions by shallow-water predatory gastropods. The identity of holes of many species of shallow-water boring gastropods has been verified in the laboratory and in the field (*e. g.*, Wiltse, 1980; Carriker, 1981; Ansell and Morton, 1987; Vermeij *et al.*, 1989; Ponder and Taylor, 1992; Peterson and Black, 1995). Because all shallow-water boring predatory gastropods examined to date have been shown to possess an accessory boring organ (ABO) (Carriker, 1981; Kabat, 1990), suspected deep-sea boring gastropods could be confirmed as borers, anatomically and histologically, by the presence of an ABO. Harasewych (1984) has thus identified a bathyal trophonid as a borer.

Although taxonomically identified naticids, muricids, and trophonids have been dredged from the deep sea, and occasional figures of boreholes in molluscan valves, presumably drilled by species in these and possibly other taxa, have been published, no systematic study of the comparative morphology of gastropod-type boreholes from the deep sea has been undertaken.

The purpose of the present study was to compare the gross morphological and light microscopical structure of boreholes of shallow-water naticids and muricids with that of presumed boreholes in molluscan shells taken at different depths in deeper regions of the oceans. The comparison was made to ascertain the degree, if any, of the resemblance of the two groups of perforations. Molluscan shells were dredged by expeditions of the Danish *Ingolf* (1895 and 1896), the Danish *Galathea* (1950-1952), and the United States *Gosnold* (1963-1964).

RECENT SHALLOW-WATER BORERS

Shell dissolution and penetration have been reviewed by Carriker *et al.* (1969) in many species of prey invertebrates. In the Mollusca, shell penetration occurs among the Bivalvia (burrowing for shelter), Gastropoda, and Cephalopoda (drilling to obtain food). Among the Gastropoda, species of boring snails are present in the families Capulidae, Naticidae, Cassidae, Tonnidae, Ranellidae, Muricidae, Marginellidae, Rapanidae, Trophonidae, Buccinidae, and Vayssiereidae; among the Cephalopoda, borers exist in at least the family Octopodidae (Orr, 1962; Wodinsky, 1969; Young, 1969; Carriker, 1981; Kabat, 1990; Ponder and Taylor, 1992; Egorov, 1993; Gordillo, 1994; Peterson and Black, 1995).

Boreholes made by snails in gastropod families (less the Cassidae) are characteristically gastropod boreholes; that is, they possess smooth walls, bevelled outer edges, decreasing diameter with depth, and are generally

circular (Carriker and Yochelson, 1968; Kabat, 1990). Boreholes of species of Cassidae have smooth exterior margins but strongly jagged inner margins (Abbott, 1968; Day, 1969). Those of the Octopodidae are highly irregular in size, shape and angle of penetration (Wodinsky, 1969). All species of borers in the Apogastropoda (less the Capulidae) penetrate the shell of prey to rasp out the flesh within; whereas the Capulidae take food from the food-gathering tract through a borehole over the tract (Orr, 1962).

RECENT SHALLOW-WATER NATICOIDEAN AND MURICOIDEAN BOREHOLES

Naticoidean gastropods commonly live and crawl through clean to slightly muddy-sandy sediment, avoiding sticky, more compacted argillaceous sediments. When they locate an infaunal mollusk (bivalve, scaphopod, or another gastropod), they burrow to its level in the sediment and drill into it there. They possess an exceptionally large fleshy foot that facilitates movement through the sediment, and with it tightly grip their prey. If the prey is smaller than the snail, the snail can completely envelope the prey with its broad foot (Kabat, 1990).

Muricoidean snails, on the other hand, generally dwell on the surface of firm to hard substrata, and prey mostly upon epifauna (bysate bivalves, such as oysters and barnacles). The size of the foot, relative to that of the shell, is very small - quite in contrast to the relatively large foot of naticoideans. Consequently, when a muricid mounts a prey to perforate it, its foot clings tightly to the surface of the prey. Most muricid species, such as *Urosalpinx cinerea* (Say, 1822) drill principally through one of the valves of prey (side drilling); whereas others, like *Muricanthus fulvescens* (Sowerby, 1834), bore at the line of contact of the two valves opposite the hinge (edge drilling), the boreholes thus assuming a long, oval outline (Carriker, 1961). Edge drilling is also done by some polinicine naticids (Vermeij *et al.*, 1989).

CHARACTERISTICS OF SHALLOW-WATER GASTROPOD BOREHOLES

Gastropod boreholes, although varying in size with the stage in the life history of individuals in a single predatory species, are characterized by a number of identifiable features. These are described here briefly as background for the following discussion of the morphology of the deep-sea boreholes.

Macroscopically, the exterior rim or margin and the interior wall of the borehole appear smooth; under magnification, radular teeth marks are visible. The inner edge of the hole (next to the soft tissues of the prey) can be sharp-lipped, smooth, or quite jagged; whereas, the exterior rim ranges from scarcely bevelled to deeply countersunk. The

exterior rim is often discolored by action of the accessory boring organ secretion (Carriker, 1981). In section parallel to the exterior surface of the shell, holes can be circular, crescent-shaped, heart-shaped, or highly irregular, but most commonly are circular, a result of the back-and-forth turning of the radula-supporting odontophore on its long axis. The depth axis of muricid boreholes is generally perpendicular to the external shell surface because of the radial symmetry of the extended muricid accessory boring organ and the perpendicular position of the longitudinal axis of its stalk to the ventral surface of the foot. Perpendicularity is also characteristic of some naticid boreholes, especially those drilled in relatively smooth-shelled bivalves. This results from the position of the accessory boring organ on the ventral tip of the naticid proboscis. Symmetry of muricid boreholes can be warped by ornamentation, growth irregularities, and differences in hardness of prey shell, resulting in oval or smoothly angular holes. Exaggerated external shell sculpture such as costae, concentric ridges, imbrications, flutings, and the like, can be reflected on the side of the borehole (Carriker and Yochelson, 1968; Kabat, 1990).

In prey shell composed of homogeneous material (Carriker, 1996), boreholes are uniformly symmetrical. However, the presence of layers of shell material of different mineral composition or hardness can result in irregularities in the diameter of the borehole (Carriker and Yochelson, 1968).

Because of the proportionally small size of their accessory boring organ and stalk, small drilling gastropods successfully penetrate only small, thin-shelled prey (Carriker, 1957; Carriker and Van Zandt, 1972). The diameter of the borehole (at the external surface of the shell) generally indicates the size of the predator; but because small adult snails also excavate holes, the size of hole does not necessarily indicate the age of the borer. Although it is not always possible to distinguish holes bored by naticids from those by muricids, the two types are quite distinctive in a populational sense: typical naticid boreholes are broadly parabolic, whether excavated in thick or thin prey shells, whereas muricid holes appear parabolic in thin prey shells, but in thicker shells the borehole assumes the characteristic cylindrical or nearly cylindrical form with a minor bevel on the exterior margin.

MATERIALS AND METHODS

Molluscan shells for the examination of holes attributed to deep-sea gastropods, were kindly loaned by Dr. Jørgen Knudsen, Zoological Museum, University of Copenhagen, Denmark. These shells were dredged during

(a) the Danish Deep-sea Expedition Round the World, 1950-1952, from the *Galathea* (Brunn, 1957b), and (b) the Danish North Atlantic voyage, 1895 and 1896, from the *Ingolf* (Jensen, 1912). A sample of shells was also generously made available by Mr. Roger B. Theroux, Northeast Fisheries Science Center, National Marine Fisheries Service, NOAA, Woods Hole, Massachusetts, United States. They were collected from the *Gosnold* during the United States Geological Survey Continental Margin Program in 1963-1964 (Emery and Schlee, 1963; Wigley and Theroux, 1981), off of the Middle Atlantic Bight region of the western North Atlantic. Specimens studied were loaned from the Specimen Reference Collection of the Northeast Fisheries Science Center, and are now housed in the National Museum of Natural History, Smithsonian Institution, Washington, D. C.

The *Galathea* shell specimens were collected at stations off of southern Africa, east of India, east of the Philippines, around Bali, and off of southern Australia, at depths ranging from 435-2690 m. Dr. Knudsen selected shells with holes from dredgings deeper than 400 m. Twelve stations were included, between 400 m and the maximum depth of 10,210 m (Bruun, 1957b) (Table 1).

Dr. Knudsen also selected *Ingolf* bivalves [all *Hyalopecten frigidus* (Jensen, 1912)] with holes in specimens collected at stations between the Faroes, Iceland, and

Table 1. Bathymetric distribution of gastropod boreholes in valves of deep-sea mollusks collected by the *Galathea*.

Sta.	Depth (m)	Coordinates	Geographic region	No. boreholes	Borehole diameter (mm)	Mollusk bored	Type borehole
99	2690	8°40'S 11°10'E	off Angola, South Africa	3	1.1, 2.0, 2.2	*Cuspidaria* sp.	muricid
137	535-570	20°04'S 11°56'E	off South Africa	1	1.9	*Venericardia* sp.	muricid
192	3430	32°00'S 32°41'E	off Durban, South Africa	2	0.8, 1.5	*Janthina*-like?	?
302	1190	19°42'N 86°48'E	Bay of Bengal	1	1.1	*Syndosmya longicallis* (Scacchi, 1834)	muricid
423	810	10°27'N 124°18"E	east of Cebu, Philippines	1	1.2	venerid-like	naticid
436	710	10°12'N 124°14'E	east of Cebu, Philippines	1	1.2	*Limopsis* sp.	muricid
436	710	10°12'N 124°14'E	east of Cebu, Philippines	2	2.5, 2.5	gastropod	naticid
436	710	10°12'N 124°14"E	east of Cebu, Philippines	2	2.8, 2.9	*Macoma*-like	naticid
478	600	8°50'S 114°55'E	south of Bali	1	0.5	*Lima* sp.	naticid
480	400	8°49'S 115°00'E	south of Bali	1	1.7 x 2.3	scaphopod	naticid
489	1160	7°38'S 116°08'E	Bali Sea	1	1.7	*S. longicallis*	naticid
490	570-545	5°25'S 117°03'E	Bali Sea	1	0.7	*Limopsis* sp.	muricid
490	570-545	5°25'S 117°03'E	Bali Sea	2	0.6, 0.6	smooth-shelled bivalve	naticid
490	570-545	5°25'S 117°03'E	Bali Sea	1	0.6	spiral-lined bivalve	muricid
554	1340-1320	37°28'S 138°55'E	Australian Bight	1	0.7	scaphopod	naticid
557	680	37°13'S 138°42'E	Australian Bight	2	0.6, 1.0	mactrid bivalve	naticid
557	680	37°13'S 138°42'E	Australian Bight	1	2.2	compressed bivalve	naticid
557	680	37°13'S 138°42'E	Australian Bight	1	3.1	pectinid bivalve	naticid

Note: Where minimum and maximum exterior diameter of the borehole differed only by 0.1 mm, the maximum diameter is recorded.

Table 2. Bathymetric distribution of gastropod boreholes in valves of deep-sea *Hyalopecten frigidus* collected by the *Ingolf*.

Sta.	Depth (m)	Coordinates	Geographic region	No. boreholes	Borehole diameter (mm)	Type borehole
102	1412	66°23'N 10°26'W	northeast of Iceland	3	1.1, 1.2, 1.5	naticid
103	1090	66°23'N 8°52'W	northeast of Iceland	1	1.5	naticid
104	1802	66°23'N 7°25'W	east-northeast of Iceland	13	0.6-1.5 *	naticid
111	1619	67°14'N 8°48'W	northeast of Iceland	1	1.5	naticid
113	2465	69°31'N 8°06'W	southeast of Jan Mayen	5	0.7-1.2	naticid
117	1889	69°13'N 8°23'W	southeast of Jan Mayen	5	1.4-2.0	naticid
118	1996	68°27'N 8°20'W	southeast of Jan Mayen	15	1.0-2.0	naticid
119	1902	67°53'N 10°19'W	northeast of Iceland	5	1.5-2.0	naticid
120	1666	67°29'N 11°32'W	northeast of Iceland	5	1.0-1.5	naticid

*Range of diameter of boreholes.

Jan Mayen, at depths ranging from 1090-2465 m. Of the 144 stations surveyed during the voyage, 80 were at depths exceeding 1000 m (T. Wolff, pers. comm.). The benthic region investigated included the North Atlantic Ridge, running from eastern Greenland to Scotland and the slopes into basins north and south of the ridge (Jensen, 1912). Dr. Knudsen sent scallop valves with holes from 13 representative stations (Table 2).

The *Gosnold* shell specimens were collected off of the Middle Atlantic Bight of the eastern coast of the United States between Cape Cod, Massachusetts, and Cape Hatteras, North Carolina (Wigley and Theroux, 1981). I examined shells dredged at depths ranging from 579-1894 m from seven stations. The number of shell pieces examined per station ranged from one to about 50. Maximum depth of stations from which shells lacking holes were examined was 2725 m (unpublished *R/V Gosnold* station list, 1964) (Table 3).

Shells from each expedition were examined under low binocular microscope magnification. Maximum and minimum exterior diameter, degree of external marginal bevelling, smoothness of the wall, and cross-sectional shape (parallel to exterior surface of the shell) of each hole were recorded. Each hole was then characterized as naticid-type, muricid-type, or of other form, following the guidelines suggested by Carriker and Yochelson (1968). Identity of prey shell or fragments, when available, was taken from sample labels. Representative boreholes from the *Galathea* and *Ingolf* collections were photographed.

There was no record of which, if any, shells examined were collected alive. Also, to what extent post-mortem transport of the shells might have occurred prior to dredging, is not possible to say.

RESULTS

THE *GALATHEA* EXPEDITION

Molluscan shells with gastropod-type holes were collected from off of southern Africa to Indonesia, and off of southern Australia (Fig. 1; Table 1). They included two atypical holes in the shell of a gastropod (probably a seguenziid vetigastropod; Fig. 2) and 23 typical gastropod-type boreholes in several other species of mollusks (Figs. 3-5).

The larger of the atypical holes, although circular, possessed a rough jagged wall (Fig. 2), lacked a bevelled exterior edge and periostracum of the shell overhung the hole slightly. The overall appearance of the hole suggested penetration by means of breaking and crushing rather than by chemical dissolution and rasping. The smaller hole (Fig. 2, left) had the same appearance.

The gastropod-type boreholes (Figs. 3-5) were of two distinct types: (a) muricid-type: circular, smooth-walled, with only a slight bevel at the exterior margin (Fig. 3), and (b) naticid-type: circular, broadly bevelled exterior edge, deeply countersunk, and inner opening smaller in diameter than the outer with sharp edges (Figs. 4-5). In the

Table 3. Bathymetric distribution of gastropod boreholes in valves of deep-sea mollusks collected by the *Gosnold* off of the eastern coast of United States.

| Sta.	Depth (m)	Coordinates	Geographic region	No. boreholes	Borehole diameter (mm)	Mollusk bored**	Type borehole
1255	1894	42°08'N 64°53'W	northern	1	1.1	*Nucula* sp.	naticid
1826	579	32°50'N 76°59'W	southern	3	0.6-1.1*	bivalves	naticid
				2	0.2, 0.3	bivalves	muricid
1829	1431	32°32'N 76°32'W	southern	1	0.5	*Nuculina* sp.	muricid
2202	623	41°27'N 65°56'W	northern	6	0.7-1.3*	*Astarte* sp.	inflated
2203	1795	41°35'N 65°43'W	northern	1	0.8	bivalve	? edges uneven
2204	1238	41°47'N 65°38'W	northern	1	1.0	*Nuculina* sp.	naticid
2210	802	42°02'N 65°33'W	northern	2	1.0, 1.8	*Astarte* sp.	inflated

  * Range of diameter of boreholes.
 ** Unidentified valves and fragments of valves.

hole in Fig. 5, the radial ridges of the pectinid shell extended from the wall of the hole, suggesting that the ridges were composed of less soluble shell material than that of the remainder of the hole. In contrast, concentric ridges of the *Macoma*-like valve in Fig. 4 did not project from the wall of the hole, probably because of the generally uniform hardness of the shell material. The external surface around the hole of the pectinid valve (Fig. 5) was leached, presenting a chalky color in a radius of about 0.5 mm, possibly the result of chemical dissolution of the surface during shell penetration.

The hole in the scaphopod shell (Table 1, Sta. 480) was oval in shape (1.7 x 2.3 mm) reflecting the roundness of the 25-mm long shell where the hole was drilled.
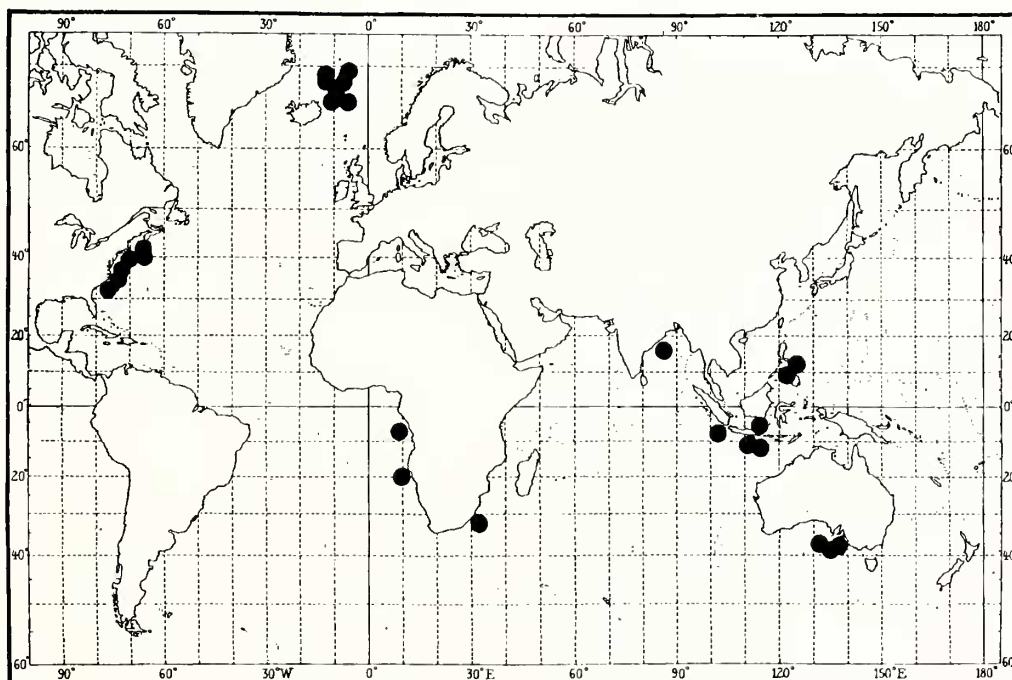
Fig. 1. Location of *Galathea* stations from off of southern Africa to off of southern Australia; *Ingolf* stations northeast of Iceland; and *Gosnold* stations off of the eastern United States, from which molluscan shells with gastropod-type boreholes were obtained.

Figs. 2-5. Gastropod bore holes. **2.** Two holes (left 0.8 mm, right 1.5 mm diameter), in shell of a presumed seguenziid vetigastropod. Below the small hole is the beginning of a second small penetration. Off of Durban, South Africa, *Galathea* Sta. 182, 3430 m. **3.** Muricid-type borehole, 1.2 mm diameter, in *Limopsis* sp., east of Cebu, Philippines, *Galathea* Sta. 436, 710 m. **4.** Naticid-type borehole, 2.9 mm diameter, in a *Macoma*-like bivalve, east of Cebu, Philippines, *Galathea* Sta. 436, 710 m. **5.** Naticid-type borehole, 3.1 mm diameter, in valve of a pectinid bivalve, Australian Bight, *Galathea* Sta. 557, 440 m.

On the whole, the range in diameter of holes was greater in naticid-type holes, 0.5-3.1 mm, than in muricid-type holes, 0.7-2.2 mm (Table 1; Fig. 6).

Most of the gastropod-type holes came from the Indonesian region (Fig. 1). Bathymetrically, most were in mollusks dredged at about 400-800 m (Fig. 6); three from an intermediate depth of about 1100-1400 m; and three, all muricid types, from 2700 m. None was found in the broad depth range of 1400-2600 m. Both naticid- and muricid-type holes were present in shallower water (400-1400 m).

THE *INGOLF* EXPEDITION

Shells of *Hyalopecten frigidus* from nine stations located northeast of Iceland (Fig. 1; Table 2), included 53

typical naticid-type boreholes (Fig. 7). There were no muricid-type boreholes.

The valves of these pectinids were thin; holes were circular, smooth, broadly bevelled on the external margin, and narrowed to a small inner opening with slightly rough edges. Small radial ridges of the shell were reflected in the wall of the holes (Fig. 7). No leeching of the shell surface was evident around the external surface of the holes. Although the degree of bevelling varied widely from one hole to another, pronounced bevelling was characteristic of all holes, even though the pectinid valves were extremely thin.

The range in external diameter of holes was 0.6-2.0 mm (Table 2; Fig. 8). The largest holes were in valves dredged at depths between 1900 and 2000 m.

Fig. 6. Bathymetric distribution of naticid-type and muricid-type boreholes in *Galathea* mollusks. (circles, naticids; squares, muricids).

Bathymetrically, most valves with holes were distributed approximately between 1400 and 2000 m; only two came from about 2500 m. Maximum numbers were dredged at depths ranging from 1700-2000 m (Fig. 8).

THE *GOSNOLD* SURVEY

Molluscan shells with gastropod-type holes were taken from dredgings at 13 stations off of the eastern United States from Massachusetts to South Carolina (Fig. 1; Table 3), and included a total of 17 holes. Of these, three were of the muricid-type, five of the naticid-type, eight were inflated (or barrel-shaped), and one was atypical.

Muricid-type holes were distinctly cylindrical with only a slight external bevel (similar to Fig. 3). Naticid-type holes were distinctly shallowly parabolic (because of the thinness of the valves), with a broadly bevelled exterior edge and inner opening smaller in diameter than the outer, with irregular sharp edges (similar to Fig. 4). In the case of the hole in a *Nucula* sp. valve (Sta. 1255) which was recently killed, the periostracum of the valve hung slightly onto the sides of the broad bevelling of the hole.

Inflated holes were present only in valves of *Astarte*

sp. The diameter of each hole was enlarged centrally and decreased toward the exterior and interior openings, giving the hole the shape in section of a small barrel (similar to Carriker and Yochelson, 1968: figs. 12-13). The external margin was only slightly bevelled.

The range in external diameter of naticid-type holes (0.6-1.1 mm) was less than that of the inflated holes (0.7-1.8 mm), whereas that of muricid-type holes was only 0.2-0.5 mm (Table 3).

Bathymetrically, muricid-type holes were found in shells dredged from 579-1431 m, and naticid-type holes from 579-1900 m. Inflated boreholes were dredged at depths of 623-802 m, and were found in the middle to northern geographic region off of the coast (Table 3; Fig. 9).

DISCUSSION

Muricid-, naticid-, and inflated-type holes in valves of mollusks dredged during the *Galathea*, *Ingolf*, and *Gosnold* voyages from depths as great as 2690 m are characterized by features so strikingly similar to those of boreholes drilled by shallow-water gastropods that they can properly be classified as gastropod boreholes. Until recently, the distribution of identified gastropod boreholes was known principally from intertidal and shallow subtidal benthic regions; the present study demonstrates that they occur bathymetrically into at least bathyal depths.

How much deeper into abyssal and hadal regions

Fig. 7. Naticid-type borehole, 2.0 mm diameter, in *Hyalopecten frigidus*, southeast of Jan Mayer, *Ingolf* Sta. 117, 1889 m.
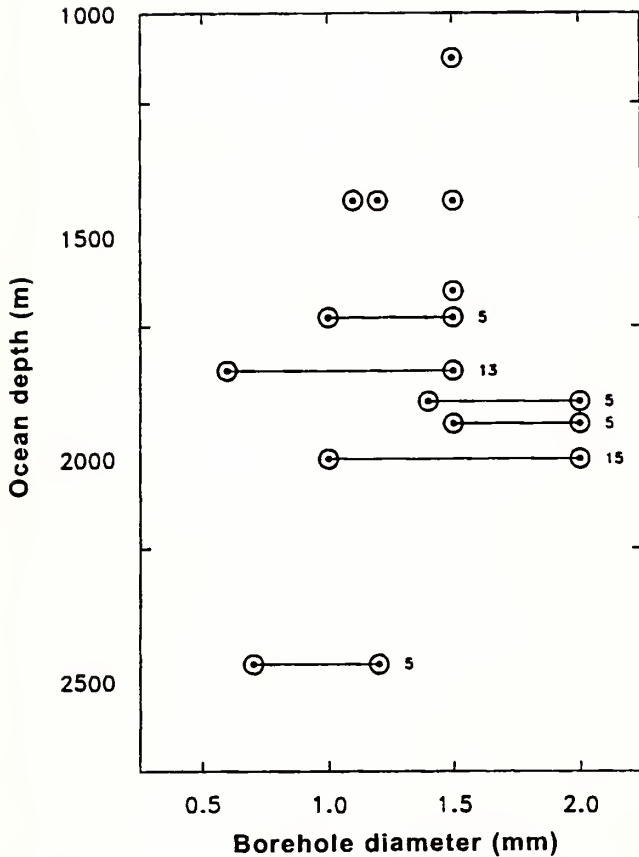
Fig. 8. Bathymetric distribution of naticid-type boreholes in *Hyalopecten frigidus* from the *Ingolf*.

boring gastropods occur, remains for future explorers to determine. The bathymetric distribution of mollusks in general, however, provides suggestions (Zezina, 1997). Deep-sea gastropods and bivalves, characteristically small (roughly 0.7-28 mm long), thin-shelled, and with reduced ornamentation (Clarke, 1962b), for example, have been dredged at all the bathyal, abyssal, and hadal depths explored to date. According to Bruun (1957a), apogastropods were taken in the Kurile Trench at 8330-8050 m; Wolff (1960) reported that gastropods and bivalves were dominant groups in 13 deep-sea trenches investigated at hadal depths exceeding 6000 m. In his exhaustive tabulation Clarke (1962a, b) listed all species of mollusks validly recorded from depths of 1830 m or more; and Knudsen (1970, 1979) recorded species of deep-sea bivalves from both abyssal and hadal regions.

The bathymetric distribution of species of Naticidae and Muricidae reported from the deep sea provides further suggestions. Schepman (1909) listed 37 species of *Natica* from bottoms in the shallower bathyal region close to *Galathea* stations from whence bored shells were collected for the present study (J. Knudsen, pers. comm.). Wolff

(1960) mentioned one to three species of Naticidae - but no Muricidae - taken at 6860 m in the Kurile-Kamchatka Trench (see also Bruun 1957a). Egorov (1993) listed *Abyssotrophon hadalis* (Sysoev, 1992) from the same trench at a depth of 6475-7230 m, as well as other species of the same genus at slightly shallower depths in this same trench. Clarke (1962a, b) recorded 21 species of naticids and 14 species of muricids from bathyal regions. And Theroux (1983), in a list of gastropods off of the eastern coast of the United States, included ten boring species. Two of the naticid species, *Natica clausa* Broderip and Sowerby, 1829, and *Euspira pallida* (Broderip and Sowerby, 1829) were dredged in water as deep as 1715 and 1170 m, respectively. McLean (1997) reported 18 caenogastropod families from the northeastern Pacific with depth records of 800 m and deeper. Because the majority, possibly all, of the species of shallow-water muricids, naticids, and trophonids studied to date are borers (Carriker, 1981; Kabat, 1990; Egorov, 1993), it is highly likely that species of these families occurring in the deep sea are likewise shell penetrators. Other deep-sea gastropod families containing boring species, such as capulids and ranellids, probably also exist.

It is puzzling that Knudsen (1964) named no species of Muricidae or Naticidae in a list of several gastropod
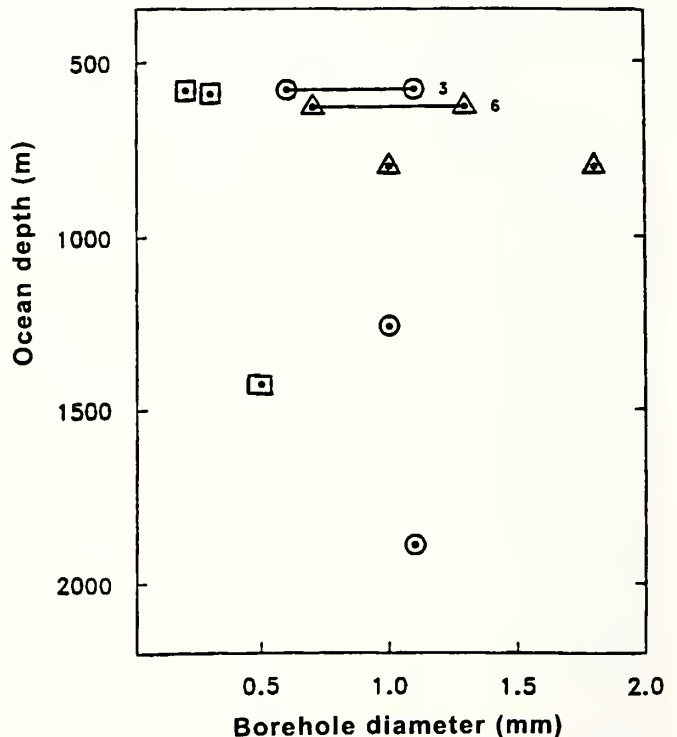

Fig. 9. Bathymetric distribution of gastropod-type boreholes in *Gosnold* mollusks. (circles, naticids; squares, muricids; triangles, inflated boreholes).

families from hadal depths exceeding 6000 m. The report-ed absence of these families could be explained by a rapid decrease in faunal diversity beyond the abyssal zone (Knudsen, 1956), by spotty distribution of gastropods on the bottom, by limited dredge size, and by the non-cos-mopolitan often endemic distribution of molluscan species in deep-sea basins (Clarke, 1962a, b).

The general paucity of muricid species reported to date in the deep sea is reflected in the low number of muri-cid boreholes (11) compared to the relatively high number of naticid holes (73; Table 4) in molluscan shells from the three voyages. The low density of reported muricid species (Wolff, 1960; Clarke, 1962a; Theroux, 1983) is probably a result of the relative scarcity of hard surfaces in the deep sea or limited dredging on hard surfaces (incompatible with dredges and trawls), rather than the effect of other environ-mental factors associated with depth. In shallow water, at least, soft substrata tend to inhibit muricid reproduction (Carriker, 1981). That some muricid-type boreholes do occur could be explained by the fact that trophonid gas-tropods, for example, are found on substrata ranging from loam, silt, and sand, to pebbles and rocks (Egorov, 1993).

The occurrence of naticid boreholes in pectinid valves collected during the *Ingolf* expedition is somewhat inconsistent with the usual habit of shallow-water naticids of drilling prey while buried under the sediment-seawater interface. Although naticids can attack bivalves on the sur-face of the sea floor (Carriker, 1981; Kabat, 1990), this is probably an uncommon behavior. Also, because naticids generally enfold prey within their foot, flattened bivalves like pectinids could hinder the shell-penetrating process. A possible explanation is that these borers were species of *Boreotrophon* that bore naticid-type holes. They possess a small foot and are able to cling to the flattened valves of pectinids; and they occur in the Iceland area (G. Vermeij, pers. comm.).

Shallow-water muricids, on the other hand, with their relatively small foot, are definitely not sedimentary

burrowers and live on the surface of firm substrata where they can attack epifaunal bivalves and barnacles. If deep-sea muricids likewise possess a small foot, one would assume that they, too, dwell on firm surfaces on, or extend-ing above, the sediment. Thus on dredgeable open sea floors where there is a scarcity of hard surfaces, few muri-cids would be expected, although some species of tro-phonids could be present there (Egorov, 1993).

The shape of inflated boreholes in the valves of *Astarte* sp. (Table 3) is something of a paradox. This type of penetration was found only in valves of this species and only in collections dredged by the *Gosnold*. The external diameter of the holes ranged from 0.7-1.8 mm (greater than that of deep-sea naticids, 0.6-1.1 mm). The larger diameter of inflated boreholes than that of deep-sea muricid bore-holes (0.2-0.5 mm) could suggest that the former were drilled by a snail species other than a muricid. The borehole drilled in *Chione cancellata* (Linné, 1767) by *Chicoreus florifer* (Reeve, 1846), in the laboratory was also large (range of external diameter 1.9-2.3 mm) (see Carriker and Yochelson 1968: pl. 2, figs. 12-13).

An explanation for the inflated middle diameter of the interior of the borehole in *Astarte* sp. and *Chione can-cellata* is unknown. Possibly the quality of shell material between exterior and interior surfaces of the valve is softer or becomes altered with time, allowing more rapid dissolu-tion of the shell there during the chemical-mechanical bor-ing process (Carriker, 1981). That composition of shell does make a difference in the diameter of a borehole, was demonstrated in boreholes drilled by *Eupleura caudata* (Say, 1822) from the New Jersey coast in valves of *Crassostrea virginica* (Gmelin, 1791) (see Carriker and Yochelson 1968: pl. 1, figs. 7-8). The diameter of these boreholes was inflated within chalky shell layers in marked contrast to that through harder foliated shell layers (Carriker, 1996). Sectioning of *Astarte* sp. boreholes and testing the hardness of the shell strata have not been done, but could provide an explanation for this form of hole.

The atypical jagged holes (Fig. 2) in the valve of the vetigastropod (Sta. 192, 3530 m; Table 1) are also a puzzle. No known shallow-water boring gastropod excavates this kind of hole in the shell of molluscan prey.

The exterior diameter of boreholes excavated by different adult species of boring gastropods varies widely. In our collection (Carriker and Yochelson, 1968), exterior diameters range from 0.6-10 mm. Boreholes drilled by snails newly emerged from the egg capsule, are 0.1 mm or less in diameter (Carriker, 1957). Boreholes in the present specimens (Table 4) ranged from 0.2-3.1 mm in outer diameter, dimensions conspicuously less than those drilled by shallow-water boring gastropods. This is not surprising, as maximum sizes of shallow-water (sublittoral) naticids and muricids are substantially larger than those of any

Table 4. Comparison of gastropod borehole data from the three expedi-tions.

	Galthea	*Ingolf*	*Gosnold*
No. muricid-type boreholes	8	0	3
No. naticid-like boreholes	15	53	5
No. barrel-shaped boreholes (inflated)	0	0	8
Range borehole diameter (mm)	0.5-3.1	0.6-2.0	0.2-1.8
Range station depth at which boreholes found (m)	440-2690	1090-2465	579-1894

bathyal or abyssal species. The size of the borehole does not necessarily indicate the age of the driller, although as a general rule smaller holes are bored by smaller snails, either small juveniles or small adults.

The present report does leave many questions unanswered. These include the maximum bathymetric distribution of gastropods that drill shelled prey, the distribution of snail borers into deep-sea polar regions (Aitken and Risk, 1988), the apparent relative scarcity of muricid boreholes, the identity and characteristics of snail species that bore holes and their method of penetrating shell. Whether boring snails dwell in the deepest reaches of hadal regions still remains unclear, although incidental observations reported earlier indicate that they could. The fact that prey shells dissolve fairly rapidly after death of the mollusk below calcium carbonate compensation depths, decreases the likelihood of evidence of drilling predation in the deep sea; gastropods with accessory boring organs at abyssal and hadal depths would be more accurate predictors of drilling predation than the absence of bored shells. The definitive identification of deep-sea boring snails, however, will require observation of the living animals in the act of drilling prey.

The observation that deep-sea boreholes examined in the present study are similar to those drilled by shallowwater boring gastropods supports Clarke's (1962a, b) hypothesis that mollusks invaded the deep sea from shallow water during the recent geologic past.

ACKNOWLEDGMENTS

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